

ARTIFICIAL INTERGENERIC HYBRIDS OF HELIANTHUS
AND VIGUIERA¹

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Helianthus and *Viguiera* are closely allied and their relationship has been discussed at some length by Blake (1918). He distinguished the two genera on the basis of the pappus, *Helianthus* having two deciduous awns rarely with intermediate squamellae and *Viguiera* having persistent awns and squamellae or lacking a pappus entirely. He also wrote of plants having a "habit" of *Helianthus* or "habit" of *Viguiera* but nowhere was this habit defined. Thus there is apparently no single character other than pappus which is fairly consistently different. Truly intermediate species are few in North America, but are represented by *H. similis* and *H. niveus*, according to Blake. In South America the situation is somewhat different and it seems probable that the 19 South American species of *Helianthus* are more closely related to the *Viguiera* of that region than they are to the North American members of *Helianthus* (Heiser, 1957).

In his treatment of *Viguiera*, Blake, realizing that presence or absence of pappus was hardly a generic character, eliminated the genus *Gymnolomnina* which was defined by its lack of pappus, and disposed of its species by placing 25 of them into various sections of *Viguiera*, and assigning the remaining eight to other genera. Of particular concern here are those former species of *Gymnolomnina* which Blake placed in the section *Helio-meris* of *Viguiera*. This group which he considered "a compact group of closely related species, well distinguished by habit and involucre" is clearly set off from other sections of the genus and at the same time is clearly morphologically distinct from *Helianthus*. The section comprises six species, five found in western North America, and the sixth, the curiously isolated *V. porteri*, known only from De Kalb, Rockdale, and Walton counties, Georgia. Chromosome numbers are known for four of the species, *V. multiflora*, *V. longifolia*, and *V. ovalis*, all $n = 8$; and *V. porteri*, $n = 17$. The latter number is the same as the basic number in *Helianthus*.

In 1957, 1958 and 1959 reciprocal pollinations of *V. porteri* were made with *H. angustifolius*, a species from the southeastern United States, which shares a number of morphological features with *V. porteri* and has an overlapping blooming period. No hybrids were secured the first two years but three were secured in the third year with *V. porteri* as the female parent. In the following year hybrids were attempted with diploid representatives of the various "sections" of *Helianthus*. No seed set resulted from reciprocal pollinations of *H. agrestis*, *H. annuus*, *H. carnosus*, *H.*

¹ This study was carried out with aid of a grant from the National Science Foundation. Special thanks are due to my research assistant, Alvin Reeves and to those mentioned in Table 2 who supplied seeds. Figures 1-16 were drawn by Nancy Clark. The chromosome count for *V. longifolia* was made by David Kramer.

laciniatus, and *H. microcephalus* with *V. porteri* but a small number of seed was secured from crosses with *H. canus*, *H. debilis* and *H. niveus* with *V. porteri* again being the female parent. At the same time crosses of another species of *Viguiera*, *V. dentata* ($n=17$, sect. *Chloracra*) were attempted with *H. atrorubens*, *H. canus*, *H. debilis*, *H. divaricatus*, *H. grosseserratus*, *H. laciniatus*, *H. microcephalus*, *H. neglectus*, *H. niveus*, and *H. occidentalis*. None of these resulted in seed set, nor did crosses of *V. porteri* with *V. dentata* and *V. multiflora*. Two hybrids, however, were secured from a cross of *V. porteri* and *V. adenophylla* ($n=17$, sect. *Chloracra*) with *V. porteri* as the female parent.

All of the hybrids between *V. porteri* and the four species of *Helianthus* superficially appear similar to *V. porteri* but careful examination shows that they are more or less intermediate for many characters or more nearly approach the condition found in *Helianthus*. Some of the more conspicuous morphological features of the hybrids and their parents based on plants grown in the greenhouse are summarized in Table 1 in which the average value is given for the numerical characters. Attention should also be called to the differences observed in the trichomes found on the corolla of the various species and the hybrids. These are illustrated for *V. porteri* (figs. 3-5), *H. debilis* (figs. 14-16) and their hybrid (figs. 8-11). Whether or not the extremely different type of bulbous trichome seen in *V. porteri* will prove of value as a "generic character" is not yet known but deserves additional study. A cursory examination of specimens of 25 different species of *Helianthus* revealed this type of trichome to be lacking. One of the most striking differences distinguishing *V. porteri* from the four species of *Helianthus*, as can be seen in Table 1, is the number of phyllaries. The involucre in *V. porteri* is best described as uniseriate whereas in *Helianthus* a second series is usually partially developed. It is worth noting that apparently all other sections of *Viguiera* are characterized by multiseriate involucres. The disk is low conic or slightly convex in *V. porteri*, nearly flat in the four species of *Helianthus* and intermediate in the hybrids. *Viguiera porteri* has fewer disk flowers per head than do the species of *Helianthus* which, of course, can be accounted for in part by the smaller disk, but more significant is the fact that the flowers are much more tightly packed in the species of *Helianthus*. Differences in stem and leaf pubescence are also found, but except to note the conspicuous trichomes at the leaf base in *V. porteri* (fig. 1) no attempt will be made to treat these in detail. Voucher herbarium specimens of the hybrids and their parents as well as those of the other species discussed here are deposited in the herbarium of Indiana University (table 2).

The intergeneric hybrids were all extremely vigorous, produced an abundance of flowers, and were nearly or completely sterile. The pollen stainability with cotton blue of the seven hybrids of *V. porteri* \times *H. debilis* ranged from 1 to 7% with a mean of 4%. The seven hybrids with *H. canus* gave a range of 0 to 13% with a mean of 4%. The *V. porteri* \times

TABLE 1. COMPARISON OF VIGUIERA PORTERI, HELIANTHUS SSP. AND THEIR HYBRIDS

	<i>V. porteri</i>	<i>P. × a.</i>	<i>H. angus- ifolius</i>	<i>p. × c.</i>	<i>H. canus</i>	<i>p. × d.</i>	<i>H. debilis</i>	<i>p. × n.</i>	<i>H. niveus</i>
Number of plants	5	3	2	7	4	5	5	3	5
Duration	annual	perennial	perennial	annual	annual	perennial	perennial	not yet known	perennial
Blooming date	Sept. 8	Sept. 12	Sept. 14	July 13	July 14	July 13	July 18	July 10	June 12
Number of rays	yellow	intermediate	orange-yellow	intermediate	orange-yellow	intermediate	orange-yellow	yellow	yellow
Length and width	12×7 mm	15×7	16×6	27×8	20×10	16×7	12×7	17×8	14×6
Disk diam.	8 mm	10	10	13.	15	13	14	10	12
No. of phyllaries	13	24	35	18	20	21	33	16	22
Length and width of phyllaries	7×1 mm	9×1	9×1	10×1½	12×2	11×2	8×2	8×1	7×2
Color of chaff tip	yellow	purple	purple	yellow	purple	faint purple	purple	yellow	yellow
No. of pappus scales	0	2	2	0	2	0-1	2	0-2	2 or more
Length of disk corolla	25 mm	34	25	39	48	35	48	37	45
Color of disk corolla lobes	yellow	red	purple	red	purple	red	purple	yellow	red
Color of stigmas	yellow	yellow	purple	red	purple	yellow with red rim	purple	red	red
L. and w. of leaves	50×8 mm	135×12	120×11	90×23	93×54	90×20	65×77	70×10	55×25
Leaf margin	entire	entire	entire	entire	serrulate	serrulate	serrate to serrulate	entire	entire

TABLE 2. SOURCE OF MATERIALS

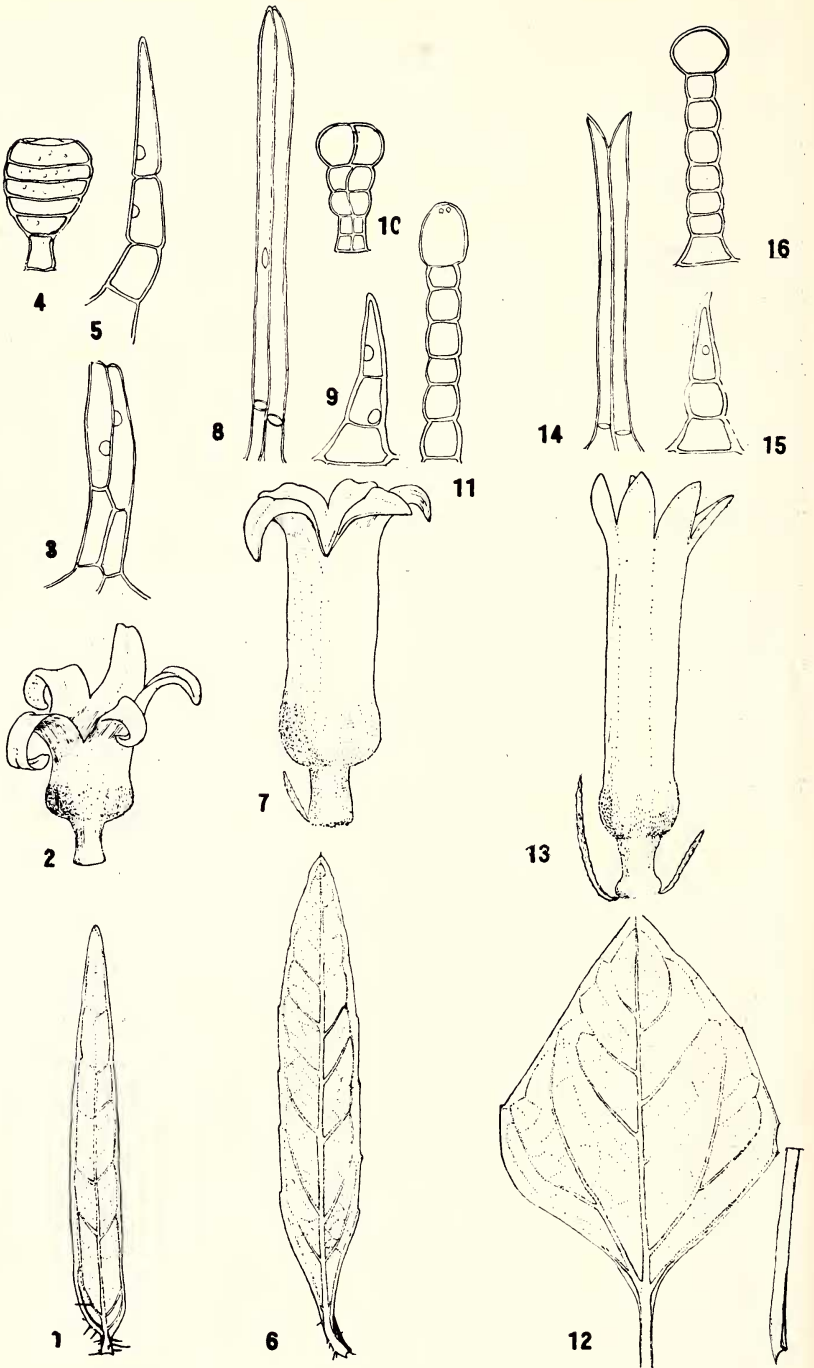
SPECIES	LOCALITY	COLLECTOR	NUMBER ¹
<i>Helianthus agrestis</i> Poll.	Polk Co., Florida	Stoutamire	1745
<i>H. angustifolius</i> L.	Marion Co., Texas	Martin	2009
<i>H. annuus</i> L.	St. Louis, Missouri	Heiser	6001
<i>H. atrorubens</i> L.	Orange Co., N. Carolina	Heiser	H551
<i>H. canus</i> (Britt.) Woot. & Standl.	Pima Co., Arizona	Heiser	4707
<i>H. carnosus</i> Small	Volusia Co., Florida	Heiser	3184
<i>H. divaricatus</i> L.	Monroe Co., Indiana	Heiser	H553
<i>H. debilis</i> Nutt. ssp. <i>debilis</i>	Volusia Co., Florida	Heiser	4665
<i>H. grosseserratus</i> Mart.	Greene Co., Indiana	Heiser	H502
<i>H. laciniatus</i> Gray	Zacatecas, Mexico	Jackson	2493 (H535)
<i>H. microcephalus</i> T. & G.	Monroe Co., Indiana	Heiser	(6024A)
<i>H. neglectus</i> Heiser	Ward Co., Texas	Clewell & Torres	H561
<i>H. niveus</i> (Benth.) Brandg.	Ensenada, Baja Cali- fornia, Mexico	Heiser	5849
<i>H. occidentalis</i> Ridd.	Lake Co., Indiana	Dale	(N1)
<i>Viguiera adenophylla</i> Blake	San Luis Potosi, Mexico	Stoutamire	2813
<i>V. dentata</i> (Cav.) Spreng	Bernalillo Co., New Mexico	Heiser	V4693
<i>V. longifolia</i> (Robins. & Greenm.) Blake	Cochise Co., Arizona	Goodding	443-61 (62V22)
<i>V. multiflora</i> (Nutt.) Blake	Bernalillo Co., New Mexico	Heiser	V4994
<i>V. ovalis</i> Blake	Cochise Co., Arizona	Goodding	416-51a (62V25)
<i>V. porteri</i> (Gray) Blake	DeKalb Co., Georgia	Duncan	(Vp)

¹ The number in parenthesis is the culture number used for some plants grown at Bloomington.

H. niveus hybrids gave counts of 9, 19, and 29%, and those with *H. angustifolius* were 5, 8, and 20%. Three-fourths of the stainable grains in the last plant were quite large and had four instead of the usual three germ pores. That these grains are polyploid seems likely and is suggested by the occurrence of two celled "tetrads" (fig. 24).

Over 100 heads of field grown hybrids of *V. porteri* × *H. angustifolius* and *V. porteri* × *H. debilis* which were examined failed to yield a single seed. Sister crosses of these hybrids as well as those of the other two combinations also failed to produce seed. All possible backcrosses, except that of *V. porteri* × *H. canus* to *V. porteri* which did not overlap in their blooming period, were attempted and all were barren with the exception that six apparently filled achenes were secured in the cross of *V. porteri* × *H. debilis* with *H. debilis* as the female parent. These seeds failed to germinate.

Meiosis was examined in two or more of the plants in all of the hybrid combinations. Acetocarmine squash preparations were utilized and these were made permanent by means of the Venetian turpentine technique.



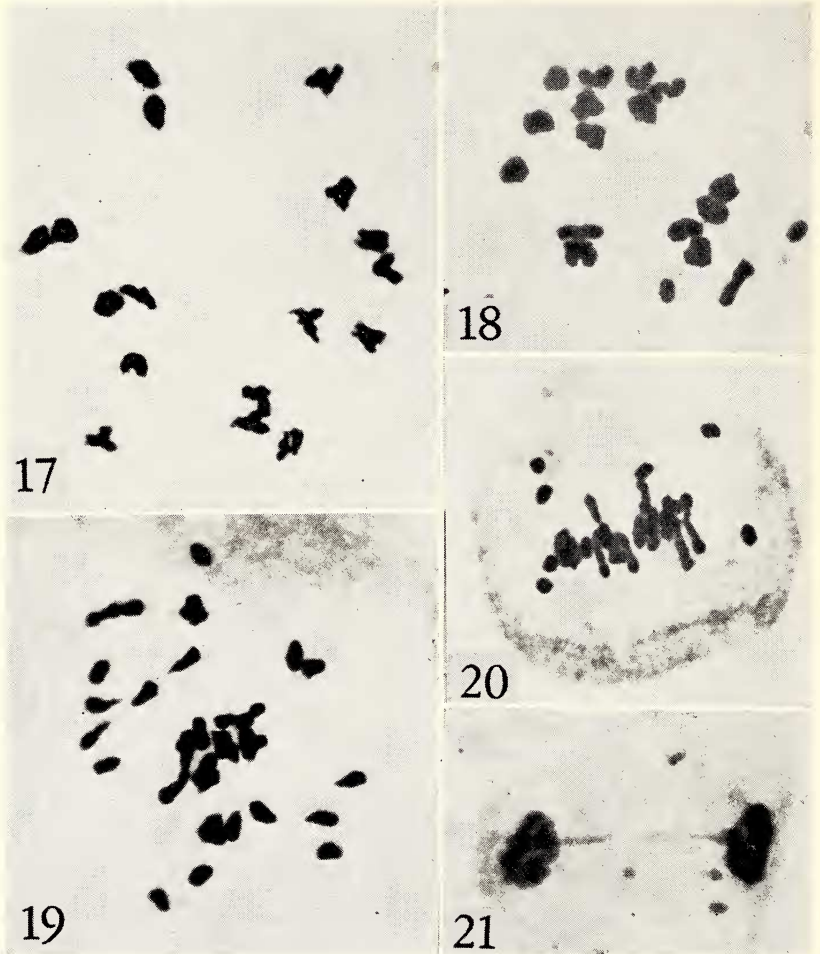
In *V. porteri* \times *H. angustifolius* over 100 slides were made and only a small number of cells were found at diakinesis. These could not be analyzed in detail but up to ten pairs of chromosomes were observed and chains were always present. At late diakinesis and metaphase I (figs. 22, 23) from six to 26 univalents were observed. Micronuclei were observed at the tetrad stage (fig. 25). In *V. porteri* \times *H. niveus* in 25 cells studied at diakinesis the number of bivalents ranged from one to ten with a mean of five. Fewer irregularities were noted in the other two hybrid combinations. In *V. porteri* \times *H. canus* 89 cells were studied at diakinesis and the following configurations were found: nine cells with 17_{II}, 11 with 16_{II} 2_I, 30 with 15_{II} and a chain of IV, nine with 15_{II} and a circle of IV, six with 15_{II} 1_{III} 1_I, one with 15_{II} 4_I, 16 with 14_{II} 1_{IV} 2_I, three with 14_{II} 1_{IV}, two with 14_{II} 1_{III} 3_I, and two with 13_{II} 1_{IV} 4_I. At metaphase univalents were uncommon, although one to three were seen in some cells. Good stages of diakinesis were rare in *V. porteri* \times *H. debilis* but four cells were seen with 17 bivalents (fig. 17). Univalents were also evident at this stage (figs. 18, 19) and from two to ten univalents were observed at metaphase (fig. 20). Bridges were observed at anaphase in all of the hybrids and were sometimes accompanied by a fragment (fig. 21).

The two hybrids secured between *V. porteri* and *V. adenophylla* were less vigorous than the intergeneric hybrids. One died before flowering and the other plant produced only a small number of flowers and these were smaller than those of either parent. Pollen stainability was 5%. Very few cells could be found for study of meiosis. Eight of these, however, showed 34 univalents, with 17 large chromosomes and 17 small chromosomes (fig. 27), and from a study of the chromosomes of the parents it appears that the 17 large chromosomes came from *V. porteri* (fig. 26). The possibility that some chromosome pairing occurs in the hybrid cannot yet be ruled out.

DISCUSSION

The difference in pairing observed in the *Helianthus-Viguiera* hybrids is of interest in connection with the presumed relationships of the species of *Helianthus* involved. Two general groups of North American sunflowers may be recognized, the "annuals" and the "perennials" (Heiser, Martin, and Smith, 1962). Hybrids within either of these groups are generally readily secured and usually show some fertility whereas hybrids between the two groups are impossible to obtain or are highly sterile. Both *H. canus* and *H. debilis* are placed in the annual group, and hybrids of these two species show moderate to good chromosome pairing with *V. porteri*,

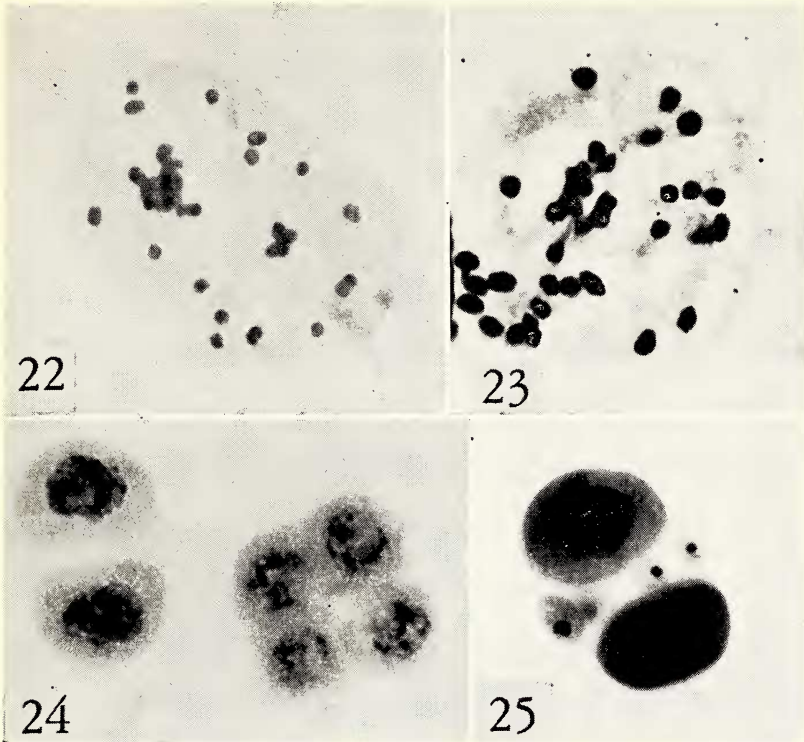
FIGS. 1-16. Leaves, disk corollas, and trichomes of *V. porteri*, *V. porteri* \times *H. debilis*, and *H. debilis*; 1-5, *V. porteri*; 6-11, *V. porteri* \times *H. debilis*; 12-16, *H. debilis*; 1, 6, 12, leaves, \times $\frac{2}{3}$; 2, 7, 13, disk corollas, \times 5; 3, 8, 14, trichomes from apex of achenes; 4, 10, 11, 16, trichomes from tube of corolla; 5, 9, 15, trichomes from throat of corolla. All trichomes, \times 18.



FIGS. 17-21. Meiotic stages in *V. porteri* × *H. debilis*, × 1200. For explanation see text.

whereas the hybrids of *Viguiera* with *H. angustifolius* and *H. niveus* show little or no pairing. *Helianthus angustifolius* is a member of the perennial group. *Helianthus niveus* has hitherto been grouped with the annuals on overall morphological similarity but it is perhaps significant that thus far it has been impossible to secure crosses of *H. niveus* with the annuals.

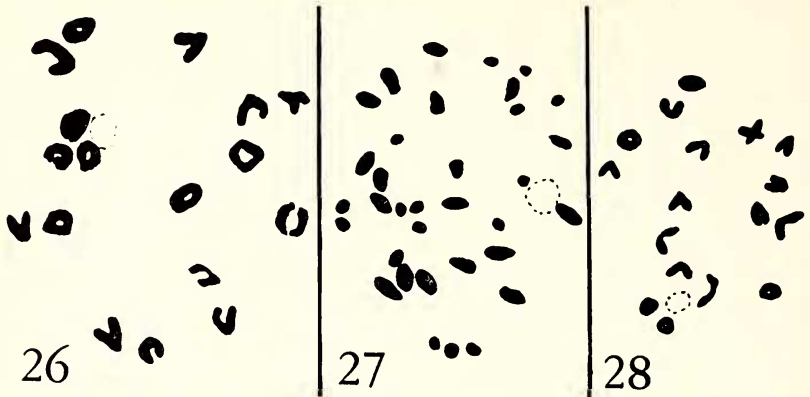
It may also be of significance that hybrids of *V. porteri* are more readily secured with *Helianthus* than with other species of *Viguiera*, and moreover, that the one intrageneric hybrid of *Viguiera*, *V. porteri* × *adenophylla*, is highly sterile and indicates considerable difference in the chromosomes of the two parents. Thus the evidence we have at present, although



FIGS. 22-25. Meiosis stages in *V. porteri* \times *H. angustifolius*, \times 1200; 22, 23, mostly univalents; 24, tetrad stage, showing two- and four-celled types; 25, pollen "tetrad" with micronuclei.

admittedly very limited in view of the large size of *Viguiera*, perhaps suggest a closer relationship of *V. porteri* to *Helianthus* than to *Viguiera*.

The securing of hybrids between *Viguiera* and *Helianthus* may bring up the question whether or not we are dealing with distinct genera. To some (Simpson, 1961) the production of a hybrid between two genera is sufficient basis for merging them. Hybrids between *Euchlaena* and *Zea* are known, and Reeves and Mangelsdorf (1942) have transferred the species of *Euchlaena* to *Zea*. Their basis for doing so, however, was on morphological grounds. The hybrids secured between *Lycopersicon* and *Solanum* by Rick (1951; 1960) are also of interest in this connection. Correll (1958) pointed out that the species of *Solanum* involved in these hybrids are morphological intermediates between the two genera, and the two have recently been united (Macbride, 1962) or reunited, for Linnaeus originally placed the tomato in *Solanum*. Kruckeberg (1962) pointed out that "the ability to make successful hybridizations between species of related genera is not sufficient to cause the joining of those species into a single genus."



FIGS. 26-28. Camera lucida drawings of chromosomes of *V. porteri*, *V. porteri* \times *V. adenophylla*, and *V. adenophylla*, \times 1200; 26, *V. porteri*; 27, *V. porteri* \times *V. adenophylla*; 28, *V. adenophylla*.

In view of the weakness of the "generic" character it may indeed eventually prove desirable to unite *Helianthus* and *Viguiera*, but for the sake of convenience, which may well enter in since there is no completely satisfactory definition of genera, there would appear to be good reason not to combine them. Moreover, there are certain other possibilities that need exploration—(1) should *V. porteri* be considered a monotypic genus? (2) should it alone be transferred to *Helianthus*? (3) should the section *Heliomeris* of *Viguiera*, either with or without *V. porteri*, be given generic status.

On the basis of the present study it might be argued that *V. porteri* should be placed in the genus *Helianthus*. It has a haploid chromosome number of 17, the same as the diploid sunflowers, whereas the three other members of the section *Heliomeris* are $n=8$, although it should be pointed out that chromosome numbers are not yet known for all members of this section. Its unique geographical position might more readily be explained if it were considered a *Helianthus* rather than a *Viguiera*. However, at present I still feel that on morphological grounds it is closer to the group with which Blake places it, so until more detailed morphological studies are made there appears to be no justification for transferring it to *Helianthus* or for erecting a monotypic genus for it. Certainly the placing of the section *Heliomeris* into the genus *Viguiera* needs reexamination. The possibility of restoring these species to a genus of their own deserves consideration.² Thus these intergeneric hybrids are of interest in stimulating an examination of the existing classification, but by themselves are hardly adequate basis for making taxonomic changes.

² Since this was written it has been found that T. D. A. Cockerell (Notes on the flora of Boulder County, Colorado. *Torreyana* 8:177-183, 1918) had already reached the same conclusions and had made formal transfers of these species, including *V. porteri*, to *Heliomeris*.

SUMMARY

Artificial hybrids of *Viguiera porteri* ($n=17$) with four species of *Helianthus*, *H. angustifolius*, *H. camus*, *H. debilis*, and *H. niveus* (all $n=17$) are described. Chromosome behavior was analyzed at meiosis and two of the hybrid combinations show a high number of univalents whereas the other two show fairly good pairing. All of the hybrids are sterile. *Viguiera porteri* has also been hybridized with *V. adenophylla*, producing a sterile hybrid showing 34 univalents at meiosis. It is pointed out that in some respects *V. porteri* appears to be more closely related to *Helianthus* than to other members of *Viguiera*. Problems in the classification of *V. porteri* are discussed, but no taxonomic transfers appear to be warranted until additional studies can be undertaken.

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NOTES AND NEWS

TRAVEL TO THE 10TH INTERNATIONAL BOTANICAL CONGRESS, EDINBURGH, AUGUST 3-12, 1964.—The Botanical Society of America has appointed a committee to receive applications and recommend grants toward the cost of travel to the forthcoming congress. Professional botanists who are citizens of the United States are eligible to apply. They need not be members of the Botanical Society. The deadline for receipt of applications is February 15, 1964 and awards will be announced on or about April 1. Application forms may be obtained from Ralph E. Cleland, Chairman of the Travel Grants Committee, Department of Botany, Indiana University, Bloomington, Indiana.